HEREDITARY REACTION-SYSTEM RELATIONS—AN EXTENSION OF MENDELIAN CONCEPTS

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The most important as well as the most consistent and intelligible series of Mendelian conceptions are those which Morgan and his associates have formulated on the basis of their extensive studies of heredity in the common fruit fly, *Drosophila ampelophila*. During the progress of their investigations they have observed the origin of over a hundred factor-mutations in this species, and they have determined the hereditary interrelations of a large number of them. They have established, for the fruit fly, the validity of the fundamental conception of Mendelism that the units contributed by two parents separate in the germ cells of the offspring without having had any effect on one another, that long and intimate association in the same chromosomal mechanism does not modify the fundamental constitution or relations in the hereditary mechanism of the units of which it is made up. They have also demonstrated that the known behavior of the chromosomes furnishes a most satisfactory basis for an explanation of the distribution of hereditary units to the germ cells. Furthermore, from the linkage-relations displayed among the factors, Morgan has succeeded not only in demonstrating that the number of groups of factors corresponds to the number of pairs of chromosomes, but he has also succeeded in preparing a map of the relative linear positions of the factors within the chromosomes. It, therefore, follows that, so far as heredity is concerned, the chromosomes are made up of a linear series of loci which bear at least some specific relation to one another as is indicated by this aggregation into chromosomes. Hereditary modifications of characters in the individual depend upon changes in the loci, a particular type of change in some particular locus corresponding to each different character-modification. Now, since a changed locus maintains the same formal relations with the other loci in the system as it does in its normal unchanged condition, it is clear that the chromosome conception of heredity furnishes a consistent explanation of the fundamental nature of allelomorphism and of the mechanistic basis of Mendelian segregation. Further the evidence of somatogenesis seems to indicate that the hereditary units form a physico-chemical reaction-system of which the elements, the loci of the hereditary system, bear more or less specific relations to one

another. In *Drosophila*, for example, the development of the normal abdomen under certain environmental conditions in spite of the presence of the factor for abnormal abdomen in the reaction system indicates the existence of compensatory relations among the factors of the system. Such compensatory relations are even more strikingly evidenced in the case of maize seedlings of the yellow-green chlorophyll reduction type. Normally these die, but under favorable conditions the system is able to overcome the disturbance incident upon the presence of the chlorophyll reduction factor and to go on and develop the normal chlorophyll coloration in the plant. Similarly, the lethal effect of changes in certain loci, the similarity in effect of different changes in the same locus displayed in multiple allelomorphism, the apparently universal significance of the multiple-factor conception of character development, and a variety of other considerations indicate that important physiological relations exist among the loci of the system, and that character expressions depend upon the reaction-system relations of Mendelian factors. The product of somatogenesis, the individual, represents the reaction end-product of such a physico-chemical system working under particular conditions; the specific hereditary differences between individuals of the same species indicate particular differences in some one or more elements in such a reaction-system. Normal Mendelian behavior, then, would follow as a result of hybridization phenomena involving a contrast between a relatively few particular differences within a reaction system which is fundamentally identical in the races under consideration. If in contrast to this type of behavior it should be possible to secure contrasts of fundamentally different reaction systems, then conceivably the elements, although playing definite parts in their own systems, might fail to establish the harmonious inter-relations which are necessary for normal development and reproduction. Such incompatibility of elements would give rise to a peculiar type of behavior in inheritance which could not well be accounted for by the customary formal treatment based on the Mendelian viewpoint. The experimental data which we have collected seem to indicate that such a situation actually does obtain in certain cases of hybridization between distinct species.

For ten years a number of species and varieties of *Nicotiana* have been grown in the University of California Botanical Garden. Among many others this collection has included *N. sylvestris* and a considerable array of varieties of *N. Tabacum*. The varieties of *Tabacum* display notable morphological differences throughout—differences so marked that to regard them as distinct species would be entirely justifiable,

even though they do show evident group relationships. On the other hand *sylvestris* apparently is monotypic and is distinctly different from the *Tabacum* group. Now, the study of a large number of varietal crosses within the *Tabacum* group has demonstrated that most characters are expressed in intermediate degrees in the F_1 hybrids and subsequent segregation in further generations indicates that these phenomena, although complex, are in accord with normal Mendelian expectation. The differences within the *Tabacum* group, therefore, apparently depend upon certain factor differences within a common reaction system. When, however, any one of this array of *Tabacum* varieties is crossed with *sylvestris*, the F_1 hybrid very nearly or completely reproduces on a larger scale the characters of the particular *Tabacum* variety concerned in the hybrid. This has been found true for a number of *Tabacum* varieties; viz. *angustifolia*, *calycina*, *macrophylla*, *macrophylla purpurea*, 'Cavala,' 'Cuba,' and 'Maryland;' descriptions and plates of which based on material grown in the University of California Botanical Garden have been given elsewhere by Setchell. The completeness of the domination of the *Tabacum* parent in the somatogenesis of these F_1 *Tabacum-sylvestris* hybrids is shown particularly in the crosses involving characters which are normally recessive in *Tabacum* variety hybrids. When *calycina*, which produces abnormal, split, 'hose-in-hose' flowers, is crossed with *Tabacum* varieties producing normal flowers, the F_1 hybrids produce the normal type of flowers with few exceptions. On the other hand in marked contrast to the type of behavior in varietal crosses, *calycina* when crossed with *sylvestris* gives an F_1 hybrid which produces only calycine flowers. Similarly, the partially parthenocarpic tendency of 'Cuba,' which is manifested in the retention and normal development of many fruits without pollination, although recessive in varietal crosses, is so impressed on the 'Cuba'-*sylvestris* hybrid that all the fruits mature normally in spite of the fact that no functional pollen is produced. Somatogensis in F_1 hybrids of *Tabacum* with *sylvestris* seems, therefore, to be dominated by the *Tabacum* system as a unit, so that any particular modification of the *Tabacum* reaction system displays its full possibilities in the development of such hybrids.

Now, if these F_1 hybrids of *Tabacum* with *sylvestris* represent the reaction end-product of two fundamentally dissimilar reaction systems, then the relations of these two systems, as manifested by the domination of the *Tabacum* system to nearly or quite the exclusion of the *sylvestris* system, indicate a rather extensive mutual incompatibility of the elements of the two systems. This deduction is borne out by the fact that the F_1 *Tabacum-sylvestris* hybrids produce only a very few

functional ovules, the number of which is apparently constant within rather narrow limits. Assuming that segregation and recombination take place normally and in accordance with the chromosome view of heredity, these functional ovules represent the *Tabacum* and *sylvestris* extremes of a recombination series, the vast majority of the members of which fail to function because they are built up from incompatible elements derived from both systems. The evidence for such a constitution of the functional ovules is furnished by the results of back-crosses of the hybrid with the parents. When the F_1 hybrid is crossed back with *sylvestris*, the progeny consists of abnormal, sterile individuals and a few typical *sylvestris* individuals which are completely fertile and breed true. On the other hand when the *Tabacum* parent is crossed back onto the F_1 hybrid the progeny consists of *Tabacum* forms some of which are completely fertile and others of which are sterile like the F_1 hybrids. The hereditary phenomena, therefore, displayed by these F_1 species hybrids confirm the conception that they represent a contrast between reaction systems, the elements of which display a considerable degree of mutual incompatibility. It follows, then, that the type of behavior displayed by species hybrids may be considered as dependent upon the degree of incompatibility of the elements of the reaction systems therein involved. Sterility in such cases is merely a logical consequence of this same incompatibility, and the degree of sterility may be regarded as an expression of its extent.

The adoption and application of such a reaction system conception to hereditary phenomena has far reaching consequences. When, for example, this conception is applied to the *Oenothera* phenomena, it at once follows that the widespread occurrence of partial sterility, the significance of which has never been definitely determined, must be of primary importance in the formulation of any consistent explanation of the hereditary phenomena displayed in *Oenothera*. Until it is possible to define clearly the exact significance of this partial sterility, it is obviously useless to attempt to apply any rigid Mendelian analysis. Moreover, the *Oenothera* phenomena belong to several different categories, three of which, at least, may be clearly distinguished. In the first place, there are some strict factor mutations in *Oenothera*, such as *rubricalyx*. These mutations depend upon a particular change in some locus in the hereditary mechanism, and they display normal Mendelian behavior when tested with the forms from which they were derived. The extensive observations of Morgan and his associates on mutation in *Drosophila*, to say nothing of other well authenticated cases in both plants and animals, seem to establish the validity and nature of this

type of mutation beyond cavil or doubt. In the second place, there is a considerable series of forms which depend upon duplication of one or more or even all of the chromosomes to the extent of tetraploidy in some forms. The particular type of behavior displayed by such forms appears to depend upon changes in the proportions of the elements within the reaction systems, rather than upon actual changes in germinal substance. In the third place, there is a complicated group of phenomena which appear to be best considered as due to complex segregation of a type analogous to that displayed in wide crosses. In contrast to the simple and definite behavior of factor mutants, the forms resulting from this segregation are often distinctly different throughout from the forms from which they arose, and when tested with them, they exhibit a complicated but orderly type of hereditary behavior. There are two facts which stand out prominently with respect to this behavior—first the mutations affect the total ontogenetic development of the individual and second they tend to recur in relatively constant ratios in certain races. The definite ratio relations in the production of 'mutant' forms, the peculiar but orderly behavior of the hybridization phenomena, and the universal occurrence of partial sterility make together a series of facts which seem at least as consistently explainable on the basis of substratum hybridity as on assumptions of general germinal change. If the conceptions applied above to the behavior of species hybrids be extended in a somewhat modified form to the *Oenothera* phenomena, the occurrence of the 'mutants' and their subsequent behavior in hybridization admit of logical arrangement and interpretation without any necessity for assumptions of extensive germinal changes.

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POINT SETS AND ALLIED CREMONA GROUPS (PART II)

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In Part I of this account[1] the ordered set P_n^k of n discrete points in a projective space S_k was studied with particular reference to its invariants, its association with a set Q_n^{n-k-2}, and its mapping upon a space $\Sigma_{k(n-k-2)}$. In this space Σ there was induced by permutation of the